

Feeding behavior and diets of Neotropical water rats, genus *Ichthyomys* Thomas, 1893

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Abstract

Observations of the feeding behavior of captive animals and dissections of the digestive tracts of kill-trapped specimens suggest that Neotropical water rats of the genus *Ichthyomys* regularly consume a wide variety of aquatic organisms, chiefly arthropods, and are not so piscivorous as their name implies. Behavioral and dietary data further indicate that crabs of the family Pseudothelphusidae may be an important food source for lowland populations of water rats; highland populations of *Ichthyomys*, however, may be largely insectivorous.

Introduction

Semiaquatic rats of the genus *Ichthyomys* are among the most unusual of Neotropical mammals, but few reliable data on their ecology or habits are available. A single fish contained in the stomach of the holotype of *I. stolzmanni*, a Peruvian form, led THOMAS (1893a, b) to infer that the rodent was piscivorous; subsequent authors have therefore referred to species of *Ichthyomys* as Fish-Eating Rats, and have even attributed the alimentary habits implied by this dubious sobriquet to other, related cricetine genera whose diets are wholly unknown. In this note we report observations on the feeding behavior of two captive specimens of *Ichthyomys*, present data on stomach contents of wild-caught examples, and discuss the probable trophic role of these rats in Neotropical streams and rivers.

Feeding behavior

The two captive animals from which our behavioral observations derive are examples of *Ichthyomys pittieri* (HANDLEY and MONDOLFI 1963). The holotype of *I. pittieri* was collected in 1958 from a small, clear mountain stream (Fig. 1) flowing through evergreen rainforest in the Cordillera de la Costa of Estado Aragua, Venezuela (BEEBE and CRANE 1947 describe the local ecology), but efforts by numerous collectors over the following 22 years failed to secure any additional specimens. In 1979 VOSS revisited the type locality and took a single adult male water rat (MBUCV [= Museo de Biología, Universidad Central de Venezuela; Caracas] I-2776), the second known specimen, in a National live trap set in shallow water beneath an overhanging rootmat at 925 m elevation. The animal was kept alive for five days in the laboratories of the Universidad Central de Venezuela at Estacion Biologica Rancho Grande. That its behavior might be observed, the rat was placed nightly in a glass 50 gallon terrarium filled to a depth of several centimeters with local soil and provided with a large, shallow enamel pan containing 1–2 cm of tap water. Food items, collected from local streams, were placed in the water or were offered the rodent with forceps. Observations totalling about 10 hours were made shortly after dusk by artificial

light on five consecutive nights. Movements and noises outside the tank elicited no apparent response from the rat. Behaviors described below were exhibited repeatedly by the animal during its period of confinement, and are here reported as though comprising a typical feeding sequence.



Fig. 1. The type locality of *Ichthyomys pittieri* in the Cordillera de la Costa, Estado Aragua, Venezuela 10° 21' N, 67° 41' W; the portion of the stream shown in the photograph is at approximately 900 m elevation (photogr. by P. KAARAKKA)

no more remained. Caddisfly (Trichoptera: Hydropsychidae), stonefly (Plecoptera: Perlidae), dragonfly (Odonata: Libellulidae) and small dobsonfly (Megaloptera: Corydalidae) larvae were eaten in this way.

Larger prey elicited other, conspicuously different responses from the rat. Tadpoles (unidentified, to 50 mm), fishes (Characidae: *Creagrutus beni*, to 55 mm standard length) and large dobsonfly larvae (to 65 mm) were pinned to the bottom of the pan with the forepaws, bitten repeatedly until moribund, and then carried out of the water to be consumed on dry land. Securing and eating large prey were often lengthy processes. Slippery animals (fish and tadpoles) appeared difficult to capture, even in the very shallow water of the pan. Dobsonfly larvae were difficult to subdue, and the rat acted several times

Upon entering the water-filled pan, the rat invariably lowered its muzzle in such a way that the tips of the mystacial vibrissae were brought in contact with the bottom of the container and began to move swiftly about in the water with the ventrally-directed whiskers sweeping a broad path before it. This evidently purposive searching behavior, characterized by direct and close application of vibrissae to substrate, was never observed while the rat was outside of water. Live prey items were attacked when they moved after having been touched by vibrissae; struggling items underfoot, however, were usually ignored as were most items (dead or alive) that did not move when touched by whiskers. Small prey (15–20 mm or less in length) were seized with the forepaws and bitten repeatedly until subdued. Usually, such diminutive items were eaten *in situ*, the rat typically crouching on its hindquarters in the shallow water with the prey held between its forepaws. Pieces of the morsel were bitten off rapidly, chewed and swallowed until

as though it had been bitten while attacking these large and formidable insects. Once carried out of the water, large prey items were held pressed to the substrate with the forepaws, seized with the incisors, and torn apart by powerful, backward jerks of the head and neck. Prey of all kinds were thoroughly comminuted by the incisors and only briefly chewed.

Behaviors described above seemed to vary chiefly with prey size inasmuch as similar responses were elicited by similar-sized prey of several species. Freshwater crabs (Pseudothelphusidae, to 50 mm carapace width), however, were attacked, subdued and



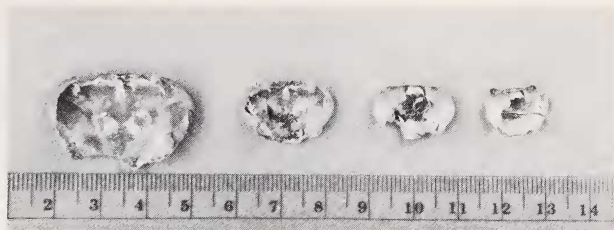
Fig. 2. *Ichthyomys pittieri* (the Rancho Grande specimen) eating a crab. Fragments of previous meals litter the foreground (photogr. by P. KAA-RAKKA)

eaten in a distinctive, stereotyped manner. When encountered by the rat, crabs usually reacted by raising and spreading their open chelae. The rodent always attacked immediately, darting at the crab with swift, lunging movements of forepaws and head until one of the claws and then the other were pinned to the substrate and bitten off at the base. The rat then seized the carapace with its forepaws (Fig. 2) and, tipping it from side to side, bit off the remaining walking legs; afterwards, the crustacean was turned upside down and the exoskeleton opened with powerful bites through the posterior margins of the carapace and abdomen. With lower incisors and tongue, the rat scooped out gills, muscle and viscera and then discarded the empty shell (Fig. 3). If the crab was a large one, the rat would frequently bite open the proximal segments of each of the detached walking legs and eat the enclosed muscle. Because the rat was sacrificed shortly after it had eaten several crabs, Voss was able to confirm by dissection that only gills, muscle and viscera had been consumed; the few small exoskeletal fragments contained in the gut would not have been identifiable had their source been unknown.

The Rancho Grande water rat evinced marked preferences for some of the aquatic organisms offered it but completely refused others. Crabs were always accepted and were eaten immediately, as were dobsonfly and dragonfly larvae. Fishes and tadpoles, however, while invariably killed and carried out of the water, were seldom eaten completely. Sometimes the rat would eat a small portion, from fishes near the caudal peduncle, from tadpoles the tail tip. Often, however, the fish or tadpole was simply carried outside the pan, dropped, and subsequently ignored. The rodent appeared unable to capture live *Colostethus collaris* (Dendrobatidae), a locally ubiquitous streamside frog, but would accept and eat dead frogs when these were provided. By contrast, *Pachychilus laevisimus* (Pachychilidae), an abundant local freshwater snail, was never eaten by the rat even when shells had been crushed prior to presentation.

The Rancho Grande rat fed voraciously; during one typical 75 minute foraging bout the rodent consumed a total of two frogs, six crabs, five dobsonfly and two stonefly larvae, and one caddisfly and one dragonfly larva.

Fig. 3. Carapaces of pseudothelphusid crabs eaten by the Rancho Grande water rat; scale in cm (photogr. by P. KAARAKKA)



The second live example of *Ichthyomys* (MBUCV I-2803) for which we have some behavioral information was collected by SILVA and VALDES at an elevation of 700 m on the northern slopes of the Cordillera de la Costa above Naiguata, Distrito Federal, Venezuela. The capture site occupies a zone of transition between the dry forests of the lower slopes and the wet forests of the higher slopes of the sierra (see STEYERMARK and HUBER 1978 for a description of local phytophysiology). The rat was captured by hand in the early afternoon as it was eating a crab (*Neopseudothelphusa fossor*) at the edge of a cement overflow canal that drained a nearby water collecting tank. The animal was maintained alive in a small wire cage for two days in the field, but died of unknown causes shortly after being transported to Caracas.

The Naiguata rat was offered local frogs (*Colostethus* sp.) and crabs (*N. fossor* and *Eudaniella ranchograndensis*). Only the crustaceans were accepted, and the sequence of rat/crab behavioral interactions observed by SILVA and VALDES were strikingly similar to those already described for the Rancho Grande rat: the rodent pinned the crab's chelae with its forepaws and then severed the limbs near their articulation to the carapace with its incisors; afterwards, the remaining four pairs of walking legs were detached, and the carapace inverted and opened with bites through the caudal margin; the soft contents both of the carapace and of the proximal limb segments were eaten. Over the two day period during which it was maintained in the field, the Naiguata rat killed and ate a total of 13 *N. fossor*, each of about 40 mm carapace width, and 1 *E. ranchograndensis* 54 mm in width. The rodent was frozen soon after its death; dissection of the digestive tract revealed that, like the Rancho Grande rat, the Naiguata specimen had ingested only a few small exoskeletal fragments.

Dissections

Additional dietary data are available from ten kill-trapped specimens: *Ichthyomys hydrobates* (Venezuela, Merida; UMMZ [= University of Michigan Museum of Zoology; Ann Arbor] 156375), *I. soderstromi* (Ecuador, Pichincha; AMNH [= American Museum of Natural History; New York] 64624), *I. tweedii* (Ecuador, Pichincha; UMMZ 126300, 155782-155788). Complete alimentary tracts were dissected from fluid-preserved carcasses and their contents removed to 70 % ethanol. Macroscopically distinctive prey fragments (tergites, antennae, mouthparts, legs, gills, etc.) were sorted and identified by matching them with corresponding parts of intact specimens collected from streams; invertebrates thus identified as prey were sent to specialists for taxonomic determination. After removal of larger fragments, the finely-masticated residuum in each gut was cleared in potassium hydroxide and hydrogen peroxide and stained with alizarine in order to heighten optical contrasts between vertebrate bone fragments (if present) and the non-osseous tissues of invertebrates.

All digestive tracts examined contained abundant arthropod exoskeletal fragments. Eight of ten tracts contained Arthropoda exclusively, but two (of *I. tweedii* from western Ecuador) contained also teeth and bone fragments of small fishes (Teleostei: Characidae). The single specimen of *I. hydrobates* from Venezuela contained stonfly (Perlidae), cad-

disfly (Hydropsychidae), and dragonfly (Aeshnidae) larvae in its gut, while the stomach and intestines of one *I. soderstromi* specimen from Quito contained only unidentifiable insect fragment. Dobsonfly larvae (Corydalidae), crabs (Pseudothelphusidae) and semi-aquatic cockroaches (Orthoptera: Blattidae) together comprised 95 % of the pooled stomach contents of eight *I. tweedii* from the Andean foothills of western Ecuador. While occasional, isolated plant fragments were encountered in the digestive tracts of some specimens, no obviously masticated boli of vegetable material or other evidences of deliberate herbivory were discovered.

Discussion

Fishes are eaten, at least occasionally, by some species of *Ichthyomys*, but data reported in this note suggest that these water rats regularly consume a wide variety of other aquatic organisms, chiefly arthropods, and are not so exclusively piscivorous as their name implies. In fact, these rodents might, in lowland situations, as appropriately be regarded as cancrivorous. That crabs constitute a regular item in the diet of *I. pittieri* is strongly suggested by the very similar, stereotyped behavioral responses elicited by crabs from rats of this species collected over 100 km apart. That crabs are also eaten by other lowland forms of *Ichthyomys* is demonstrated by their occurrence in the digestive tracts of *I. tweedii* from western Ecuador.

The lotic waters of the Neotropical lowlands are rife with decapod Crustacea, and it would be remarkable indeed if these invertebrates were not often included in the diets of carnivorous semiaquatic mammals such as water rats. Shrimps and crayfishes as well as crabs are abundant in the swamps and slower-moving watercourses of the coastal plains and river basins, but in the rocky brooks and streams of the Andean foothills and associated sierras from which most examples of *Ichthyomys* have been taken, the dominant decapods are crabs of the family Pseudothelphusidae (PEARSE 1911; HOLTHUIS 1959; FITTKAU 1964; PATRICK 1966; RODRIGUEZ 1980). Pseudothelphusids are conspicuous elements of the faunas of streams in which they occur. Small crabs frequent the wet streambanks and shallow riffles where they can be observed foraging at all hours; adults appear to be more nocturnal in their habits, and can be discovered at the bottoms of deep pools, beneath rocks and in excavated burrows along the water's edge or even wandering far from streams (CRANE 1949; WEIBEZAHN 1952; VOSS, unpubl. field notes). Armed with formidable crushing or cutting chelae, even small pseudothelphusids can deliver a painful pinch, and it is not surprising that the live *Ichthyomys* specimens we observed exhibited distinctive behaviors for despatching these crustaceans.

While crabs may comprise an important item in the diets of *Ichthyomys* populations in neotropical lowland and foothill situations, however, it is unlikely that they do so at very high elevations from which decapods may regularly be absent. Of 58 streams sampled by the senior author in the course of fieldwork from 1978 to 1980 in Ecuador and Venezuela, decapod crustaceans were found to be present in 26 watercourses sampled below 1500 m elevation, but were not encountered in 29 streams sampled above 1700 m; the highest elevation at which decapods were taken was at 1643 m in western Ecuador. Similarly, PEARSE (1916) recorded four species of *Pseudothelphusa* from streams in the foothills of the Sierra Nevada de Santa Marta, Colombia between 770 and 1540 m, but found no decapods in the cold brooks at 2550 m in the same mountains. In Venezuela, Pseudothelphusid crabs are the only decapods that occur regularly at elevations above 500 m, but records from altitudes exceeding 2000 m are apparently unknown (RODRIGUEZ 1980). Some highland populations of *Ichthyomys* as, for example, *I. soderstromi*, might therefore be almost exclusively insectivorous, and in this respect may resemble species of related cricetine genera that also inhabit streams at high elevations (HOOPER 1968; VOSS, in prep.).

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Zusammenfassung

Ernährungsweise und Nahrung der neotropischen Wasserratte, Genus Ichthyomys Thomas, 1893

Beobachtungen an gefangenen Tieren und Untersuchungen am Verdauungstrakt von Museumsmaterial ergaben, daß neotropische Wasserratten der Gattung *Ichthyomys* gewöhnlich eine große Vielfalt aquatischer Organismen verzehren, hauptsächlich Arthropoden. Sie sind demnach nicht in dem Maße piscivor, wie aus dem Namen zu schließen ist. Die Beobachtungen und Nahrungsanalysen weisen außerdem darauf hin, daß für die Flachland-Populationen Crustaceen der Familie Pseudothelphusidae eine bedeutende Nahrungsquelle darstellen. Hochland-Populationen von *Ichthyomys* scheinen demgegenüber stärker insectivor zu sein.

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